Seasonal changes in mycorrhizal and fibrous-textured root biomass in 23- and 180-year-old Pacific silver fir stands in western Washington

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Seasonal changes in mycorrhizal and fibrous root biomass were examined in 23- and 180-year-old *Abies amabilis* (Dougl.) Forbes stands. Both stands had similar patterns of change in mycorrhizal root biomass with the lowest level in the summer and highest in the fall. The fall peak of fine root biomass was the result of increased mycorrhizal and not fibrous root biomass. High levels of active mycorrhizal root biomass were measured during the winter months under a snowpack at soil temperatures of 1°C. In both stands mycorrhizal roots comprised the largest proportion of the weight of fine roots during the winter (29%) and the lowest during the summer (2%). Except during early summer, the old stand had significantly higher levels of mycorrhizal root biomass in comparison to the young stand throughout the year.

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L'étude porte sur les variations saisonnières de la biomasse racinaire sous forme d'ectomycorhizes et de racines fibreuses dans des peuplements d'*Abies amabilis* (Dougl.) Forbes, âgés respectivement de 23 et 180 ans. Les deux peuplements montrent des patrons de variation similaires avec un minimum de biomasse racinaire en été et un maximum en automne. Le maximum observé à l'automne résulte d'une augmentation de la biomasse ectomycorhizienne et non de celle des racines fibreuses. Les mesures effectuées pendant les mois d'hiver sous un couvert de neige et une température du sol de 1°C, montrent des quantités élevées de biomasse racinaire ectomycorhizienne active. Dans les deux peuplements, les ectomycorhizes atteignent la plus grande proportion (29%) du poids des racines fines pendant l'hiver, alors qu'elles en constituent le minimum en été (2%). Sauf au début de l'été, le peuplement âgé possède des quantités significativement plus élevées de biomasse ectomycorhizienne, comparativement au jeune peuplement, tout au cours de l'année.

[Traduit par le journal]

Introduction

Reviews of root biomass production in different ecosystems have been published by Santantonio et al. (1977), Coleman (1976), and Lyr and Hoffman (1967). However, fine roots, which include mycorrhizae, have virtually been ignored in most studies. Yet Harris et al. (1977) found that fine root production can be very large and can account for about 40% of total net production.

Only a few studies have examined seasonal changes in fine root production. These were carried out in a mixed deciduous forest in Tennessee (Edwards and Harris 1977), in a young Scots pine stand in coastal Sweden (Persson 1978), and in Douglas-fir stands in western Washington (Keyes 1979). Fogel and Hunt (1979), Harvey et al. (1978), and Twaroski (1963) also examined seasonal changes in the biomass of mycorrhizal roots. However, seasonal changes in the biomass of fine or mycorrhizal roots with increased stand age have not been determined.

The objectives of this study were (1) to compare seasonal changes in active mycorrhizal root tip biomass in 23- and 180-year-old Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) stands; (2) to compare biomass of mycorrhizal to fine fibrous roots (≤2 mm) in both stands; and (3) to determine what proportion of the total fine roots (≤2 mm) are composed of mycorrhizal roots.

Materials and methods

Study area

The 23- and 180-year-old Pacific silver fir stands were located at the Findley Lake research area, on the City of Seattle's Cedar River Watershed about 80 km southeast of Seattle, WA, U.S.A. (Fig. 1). The research sites are located at an elevation of 1150 m. The two research sites are separated by a distance of approximately 3 km.

Most of the annual precipitation (230 cm) at the Findley Lake site occurs as snow. Winter snow accumulations are commonly over 3 m deep. Only 10% of the annual precipitation falls during the summer months. The mean annual temperature for the Findley Lake area is 5.5°C, with a January average of −3.2°C and July average of 14.4°C (U.S. Weather Bureau, Stampede Pass Station). The conifer growing season is very short with an average of 130 days between spring bud swell and the first hard autumn frost.

Soils of the stands are derived from ca. 6 cm of volcanic ash overlying andesitic glacial till (Ugolini et al. 1977). The mean forest floor depth is 4.5 cm in the young stand and 7.0 cm in the mature stand.

The young stand contains 110 500 stems/ha while the mature stand has 510 stems/ha. The young stand is almost entirely Pacific silver fir. In the mature stand, Pacific silver fir is the dominant tree species, constituting 80–85% of all tree biomass. Associates of Pacific silver fir in the mature stand are *Tsuga mertensiana* and *Tsuga heterophylla*. *Vaccinium ovalifolium*,

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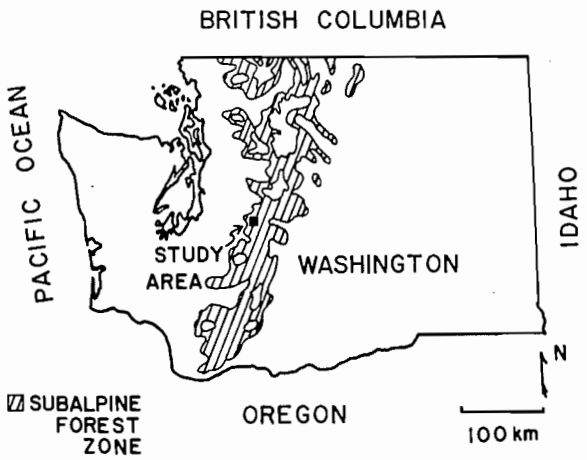

FIG. 1. Map showing location of the study area.

V. membranaceum, and *Sorbus sitchensis* are common understory shrub species. Common ground layer species are *Xerophyllum tenax*, *Clintonia uniflora*, *Cornus candensis*, *Rubus pedatus*, *Tiarella unifoliata*, and *Achlys triphylla* in both stands. These stands are both typical of *Abies amabilis* zone forests of Washington in terms of soils and vegetation (Franklin and Dyrness 1973).

Environmental measurements

Soil water potential was determined using the filter paper method described by Fawcett and Collis-George (1967). Soil water potential was determined every 2 weeks during the snow-free period in both stands. Values given in this paper are for the forest floor layers; mineral soil horizons had higher water contents throughout the growing season.

Soil temperatures were monitored using thermosensitive diodes calibrated to the nearest 0.1°C. These were coupled through a resistance bridge circuit to an automatic scanner and data recording system. Soil temperatures were measured every 2 min, integrated over a 1-h period and stored on magnetic tape for computer processing and summarization.

Root core sampling

Ten intact soil cores per sampling were obtained from each stand using a sharp-edged steel tube (3.6 cm inside diameter) hammered (approximately 25 cm) into the ground. The same procedure for obtaining cores during the snow-free period was used during the winter. The steel tube was hammered through the snow pack to the B horizon. Preliminary examination revealed that less than 1% of the conifer fine roots were located below this horizon which lay at about 25 cm depth. Cores were transferred to plastic tubes, capped, and transported to the laboratory. All cores were kept at 3°C until processed. Because of the detailed and labor-intensive root sorting required, it took 2 months to process one sampling set. Thus, samples were subject to whatever respiration weight loss occurred during this interval. Cores were separated into litter and mineral soil horizons. All mineral soil samples were washed manually over a 1-mm mesh size nylon net using a gentle flow of distilled water. Virtually no loss of roots occurred through the sieve. After washing, the samples were transferred to water-filled petri dishes and root tips were removed using watchmaker's forceps. A dissecting microscope (× 60) was used to reexamine residual material on the plates for root tips missed during the preliminary visual sorting and also to count active conifer fine root tips. Fine roots were entirely hand-sorted from all forest floor samples. As the conifer fine roots were counted, they were immediately transferred into small plastic vials. Total active conifer roots were dried in the vials at 75°C for 48 h. Roots from each horizon were separately dried and weighed. Root sample weights are not based on ash-free weights since they were later used for nutrient analyses. There was no difficulty separating roots of understory species from those of conifers; morphology and color of understory roots were distinct from those of conifers.

Mycorrhizal root tip biomass was calculated from counts of mycorrhizal root tip number multiplied by a predetermined mean dry weight of an average mycorrhizal root tip. Based on 10 groups of 40 individual mycorrhizal root tips, this mean weight was found to be 0.11 ± 0.02 mg. Biomass of conifer fibrous-textured roots was determined by subtracting the mycorrhizal root tip weight from the total conifer fine root weight.

Root tips were considered mycorrhizal if they macroscopically were ensheathed by a mantle of fungal hyphae. They also possessed a Hartig net when examined microscopically. The characteristics described by Harvey et al. (1976) and Marks et al. (1968) were used to distinguish between active and inactive mycorrhizal root tips. Only active roots were counted. Microscopic examination of root segments, using a freezing microtome, was conducted throughout the study to supplement macroscopic analyses. Roots were chosen at random and checked microscopically for mycorrhizal development and also as a verification of the visual classification of roots as active or nonactive.

Results

Environmental data

Soil temperature and water potential data are given in Fig. 2 for the Findley Lake Research area. The presence of the stable snow cover from the end of November 1978 to May 1979 maintained the soil temperature at a relatively constant 1°C. Snow melt at the end of April 1978 and the end of June 1979 resulted in a rapid rise in soil temperatures (Fig. 2). The young stand had greater moisture stress (−0.5 bars (1 bar = 10^5 Pa)) in comparison with the mature stand (−0.04 bars) during the driest time of the year in late summer (Fig. 2). However, neither stand experienced severe moisture stress during the growing period.

Mycorrhizal root biomass

Seasonal changes in mycorrhizal root biomass in the 23- and 180-year-old stands are presented in Fig. 3. Both stands had similar patterns of change in root biomass. In both stands, the lowest level of mycorrhizal root biomass occurred during the beginning of summer, and the highest in early fall.

In the 23-year-old stand, there was no significant difference in the amount of mycorrhizal root biomass measured between May and July 1978, between September and December 1978, and between March 1979 and April 1978. The 23-year-old stand appeared to maintain similar levels of mycorrhizal root biomass during the fall and winter months; however, unlike the old stand, a significantly decreased level of mycorrhizal root biomass was observed in early spring.

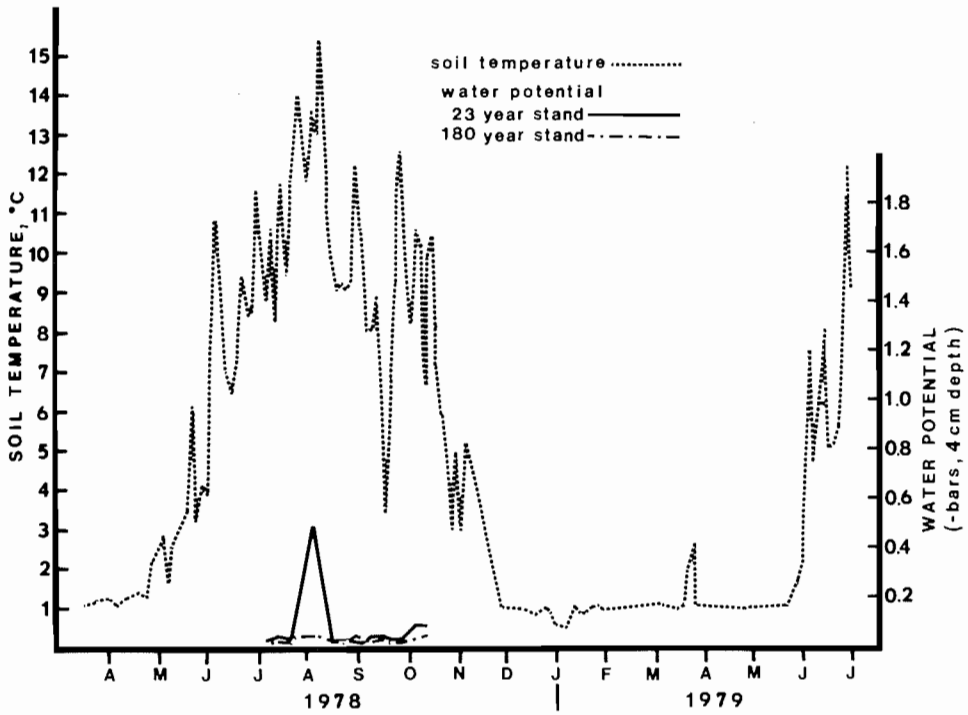

FIG. 2. Soil temperature and water potential for the Findley Lake research area.

The 180-year-old stand was characterized by having very similar levels of mycorrhizal root biomass during fall, winter, and spring. There was no significant difference in the amount of mycorrhizal root biomass measured in April, September, December 1978, and March 1979 in the old stand. The root activity measured in April and December 1978 and March 1979 occurred while the forest floor was covered with snow and soil temperatures fluctuated around 1°C.

In most cases, the 180-year-old stand had significantly higher mycorrhizal root biomass levels in comparison to the 23-year-old stand. Only during the period of lowest mycorrhizal root biomass, in May 1978, was there no significant difference in the mycorrhizal root biomass measured between the two stands.

Mycorrhizal and fibrous root biomass

The 23-year-old stand

No significant differences in the amount of mycorrhizal root biomass were measured throughout the study period between the forest floor and A horizon in the 23-year-old stand (Fig. 4). However, significantly higher levels of fibrous root biomass were measured in the A horizon in comparison to the forest floor through the 1-year study period.

During the peak of root growth in the fall, the increase in fine root biomass is the result of increased mycorrhizal and not fibrous root growth. The increase in mycorrhizal root biomass observed in the forest floor and A horizon from July to September 1978 occurred when fibrous root biomass was showing no change or decreasing slightly (Fig. 4). Very little fluctuation in fibrous root biomass in

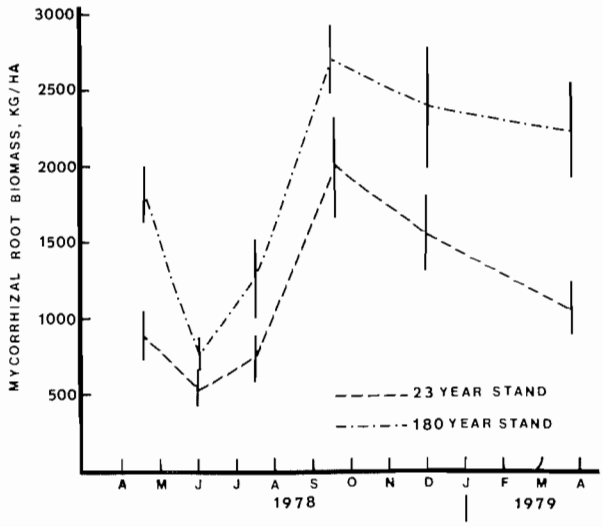

FIG. 3. Seasonal changes in mycorrhizal root biomass in the 23- and 180-year-old Pacific silver fir stands. Values were obtained from summing up mycorrhizal biomass from the forest floor and mineral soil horizons (mean ± 1 SE).

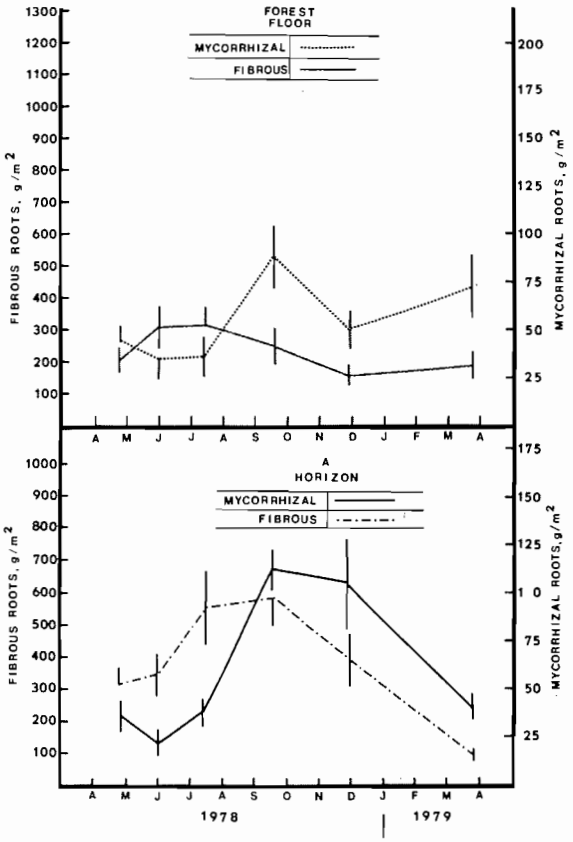

FIG. 4. Seasonal changes in mycorrhizal and fibrous root biomass in the forest floor and A horizon in the 23-year-old Pacific silver fir stand (mean ± 1 SE).

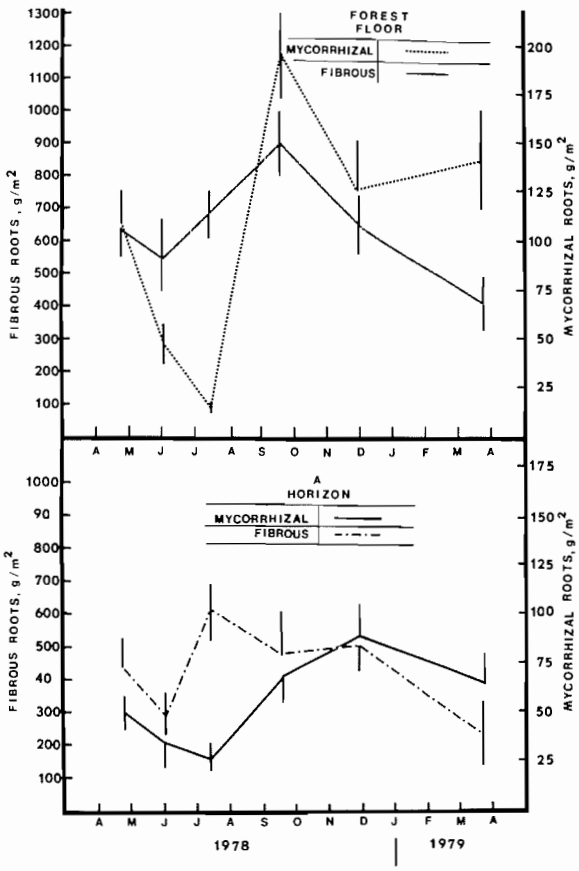

FIG. 5. Seasonal changes in mycorrhizal and fibrous root biomass in the forest floor and A horizon in the 180-year-old Pacific silver fir stand (mean ± 1 SE).

the forest floor was observed during all the sampling times. However, fibrous root biomass was significantly different in the A horizon from one sampling time to the next.

The 180-year-old stand

Significant differences in the amount of mycorrhizal and fibrous root biomass were measured throughout the study period between the forest floor and A horizon in the 180-year-old stand (Fig. 5). Generally higher levels of fibrous and mycorrhizal root biomass were measured in the forest floor in comparison with the A horizon.

The increase in fibrous root biomass from May to July 1978 in the forest floor and A horizon occurred when no change or a decrease in mycorrhizal root biomass was measured.

Mycorrhizal and fibrous root biomass peaked in September in the forest floor in the mature stand. However, mycorrhizal root biomass peaked in December and fibrous root biomass in June in the A horizon. There was no significant change in mycorrhizal root biomass from December 1978 to March 1979 in the forest floor and A horizon, while a significant decrease in the fibrous root biomass was observed during this time in both stands.

Proportion of mycorrhizal root to total fine root biomass

In both stands mycorrhizal roots comprised the largest proportion of the weight of fine roots during the months when snow covered the forest floor (Fig. 6). The increase in the proportion of the weight of fine roots composed of mycorrhizal roots starts during the fall peak of root growth and continues to increase during the winter months. Mycorrhizal roots appear to make up the smallest proportion of the weight of fine roots during the summer months. The proportion of fine root biomass composed of mycorrhizal root biomass fluctuates from a low of 2% to a high of 29%.

Discussion

Mycorrhizal root biomass

Similar seasonal patterns of changes in mycor-

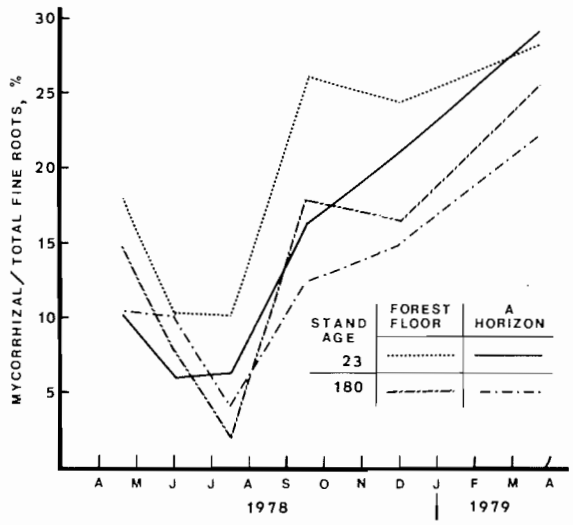

FIG. 6. Proportion of mycorrhizal to total fine root biomass in the forest floor and A horizon in the 23- and 180-year-old Pacific silver fir stands.

rhizal root biomass occurred in both stands. Lowest level of mycorrhizal root biomass occurred during the summer months and the highest during the fall and winter. Highest mycorrhizal root biomass was measured when the forest floor was covered by a consolidated snow pack. This was also the time in which mycorrhizal roots made up the highest proportion of the weight of fine roots (from 12 to 29%).

Twarowski (1963) observed in a spruce stand in Poland a similar pattern of mycorrhizal root activity. He noted that the highest percentage of living mycorrhizae occurred during autumn and the beginning of winter, providing the snow was deep enough to keep the soil from freezing.

Seasonal changes in total mycorrhizal fragments were studied by Fogel and Hunt (1979) in a Douglas-fir stand in western Oregon. No definite seasonal pattern of mycorrhizal growth was apparent in their study. The mild winters characteristic of their study plot could explain the lack of definite seasonal changes in the number of mycorrhizal fragments.

Fine root dynamics were also studied by Persson (1978) in a *Pinus sylvestris* stand in central Sweden. He monitored conifer roots of less than 1 mm diameter in which most of the root tips were ectomycorrhizal. Unfortunately the soil was frozen during the winter and no sampling was attempted during this time. Peaks of fine root activity were measured during the first sampling in April and also in June and August. This contrasts with the Pacific silver fir stands studied in Washington, where only one major peak of root activity was observed. The lowest level of root activity was measured in July which compares with the low summer activity measured in the Pacific silver fir stands.

Different patterns of mycorrhizal root growth were also measured by Harvey et al. (1978) in a Douglas-fir - larch forest in western Montana. They observed a high peak of activity during late spring and a low level of activity during the fall and winter. The lack of mycorrhizal root activity observed by Harvey et al. (1978) during the fall and winter could be explained if the soil was frozen at this time. Not enough environmental data were presented by Harvey et al. (1978) to determine if this was the case.

Low soil temperature is often deemed responsible for limiting root growth during the winter months (Lyr and Hoffman 1967). It appears that if the soil is kept from freezing (e.g., as a result of snow insulation), root activity can continue during these months. The presence of the mycorrhizal association may be critical for this winter activity. The extent of root activity may also be modified by the specific fungus forming the mycorrhizal association during this time of year. It was observed during this study that some mycorrhizal fungal species were more active at certain times of the year. Such seasonal variation in the dominance of the mycorrhizal fungus can be very important since some fungi are more effective than others in promoting plant growth (Theodorou and Bowen 1970).

The low level of mycorrhizal root biomass during the summer months cannot be explained by increased moisture stress present during these months. Even though very little precipitation input occurred during these months, moisture stress (−0.5 bars) did not reach a level that would have affected the growth of the trees.

Providing environmental factors (e.g., moisture) are not limiting root growth during the summer, decreased root activity may be explained by fewer carbohydrates being available to the root systems during periods of rapid shoot growth. Studies that have followed photosynthate translocation to the root systems of plants have shown general seasonal patterns of carbon allocation (Gordon and Larson 1968; Nelson 1964; Schier 1970; Shiroya et al. 1966; Ursino and Paul 1973; Webb 1977; Ziemer 1971). Root growth usually precedes budbreak (Gordon and Larson 1968). As buds swell and break, root activity slows down and export of carbon assimilates to the roots is reduced (Gordon and Larson 1968). Translocation then resumes to the roots when photosynthate in new needles exceeds needle or shoot requirement (Gordon and Larson 1968). Krueger and Trappe (1967) observed with nursery

grown Douglas-fir seedlings this alternating pattern of root and shoot growth. They also observed that starch concentrations increased earlier in roots than shoots and the timing of this increase occurred with the onset of new root growth. Starch concentrations reached a peak in shoots prior to bud swell and then decreased with budbreak and subsequent shoot growth. The primary source of carbohydrates to the fungus forming the mycorrhizal association is from the host plant (Harley 1969; Lewis and Harley 1965; Melin and Nilsson 1957; Shiroya et al. 1962; Wedding and Harley 1976). Therefore, seasonal changes in carbon distribution within plants will result in seasonal differences in the amount of carbohydrate potentially available to maintain mycorrhizal fungi. The availability of sucrose has been shown to be significantly correlated with ectomycorrhizal development (Marx et al. 1977). The susceptibility of short roots to ectomycorrhizal infection increased with increased concentration of soluble sugars (Marx et al. 1977).

The fall and winter peak in mycorrhizal root activity may be a response to the increased level of nutrients that are available during these months. Vogt et al. (1980) determined that the greatest weight loss of needles in litterbags in the mature stand occurred during the fall and winter months with no summer weight loss. Further research needs to be conducted to determine if the patterns of mycorrhizal root growth are a result of seasonal patterns of nutrient availability and(or) a response to patterns of carbohydrate movement within the plants.

Mycorrhizal and fibrous root biomass

Changes in fibrous and mycorrhizal root biomass generally did not occur at the same time. The peaks of fine root growth observed during the fall in the stands were predominantly due to increasing mycorrhizal and not fibrous root biomass. Fibrous root biomass increased and peaked during the summer months, except in the forest floor of the 180-year-old stand in which fibrous and mycorrhizal root biomass both reached a peak during fall.

A certain biomass of fibrous roots may be required to maintain the weight of mycorrhizal root tips. The increased weight of the mycorrhizal roots in relationship to the total fine roots (29% of fine root weight) during the fall and winter months may result in a higher carbon cost to the host tree to maintain them. When less carbon is being translocated to the root systems because of shoot growth, there is a decrease in the proportion of fine roots that are composed of mycorrhizal root tips (a low of 2% of the weight of fine roots). Fibrous root growth then appears to increase, eventually followed again by increased mycorrhizal root growth.

A similar pattern of fibrous and mycorrhizal root growth was observed by Sinclair (1974) with Douglas-fir nursery-grown seedlings. He observed an increase in the number and frequency of mycorrhizal roots in early May even though no increase in mean root weight was detected. By July and August the number of mycorrhizal roots increased in direct proportion to root weight.

In summary, the highest levels of mycorrhizal root biomass were observed during the fall and winter in both the 23- and 180-year-old stands. This activity continued under the winter snow pack at temperatures of 1°C. During the winter months, mycorrhizal roots also constituted the highest proportion of the weight of fine roots (29%). This activity may be a response to increased levels of available nutrients or to higher levels of photosynthate translocation to the root systems during these months.

The lowest level of mycorrhizal root biomass, measured during early summer, coincided with the time period in which mycorrhizal roots constituted the lowest proportion of the weight of fine roots (2%) in both stands.

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COLEMAN, D. C. 1976. A review of root production processes and their influence on soil biota in terrestrial ecosystems. *In* The role of terrestrial and aquatic organisms in decomposition processes. *Edited by* J. M. Anderson and A. MacFadyen. Blackwell Scientific Publications, Oxford. pp. 417-434.

EDWARDS, N. T., and W. F. HARRIS. 1977. Carbon cycling in a mixed deciduous forest floor. Ecology, **58**: 431-437.

FAWCETT, R. G., and N. COLLIS-GEORGE. 1967. A filter-paper method for determining the moisture characteristics of soil. Aust. J. Exp. Agric. Anim. Husb. **7**: 162-167.

FOGEL, R., and G. HUNT. 1979. Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. Can. J. For. Res. **9**: 245-256.

FRANKLIN, J. F., and D. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-8.

GORDON, J. C., and P. R. LARSON. 1968. Seasonal course of photosynthesis, respiration and distribution of ^{14}C in young *Pinus resinosa* trees as related to wood formation. Plant Physiol. **43**: 1617-1624.

HARLEY, J. L. 1969. The biology of mycorrhiza. Leonard Hill, London.

HARRIS, W. F., R. S. KINERSON, JR., and N. T. EDWARDS. 1977. Comparison of below-ground biomass of natural decid-

uous forests and loblolly pine plantations. *In* Proceedings: The below-ground ecosystem: a synthesis of plant-associated processes. *Edited by* J. K. Marshall. Range Science Department, Science Series No. 26. Colorado State University, Fort Collins, CO. pp. 29-37.

HARVEY, A. E., M. F. JURGENSEN, and M. J. LARSEN. 1978. Seasonal distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. For. Sci. **24**: 203-208.

HARVEY, A. E., M. J. LARSEN, and M. F. JURGENSEN. 1976. Distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. For. Sci. **22**: 393-398.

KEYES, M. R. 1979. Seasonal patterns of fine root biomass, production and turnover in two contrasting 40-year-old Douglas-fir stands. Master's thesis, University of Washington, Seattle, WA.

KRUEGER, K. W., and J. M. TRAPPE. 1967. Food reserves and seasonal growth of Douglas-fir seedlings. For. Sci. **13**: 192-202.

LEWIS, D. H., and J. L. HARLEY. 1965. Carbohydrate physiology of mycorrhizal roots of beech. III. Movement of sugar between host and fungus. New Phytol. **64**: 256-269.

LYR, H., and G. HOFFMAN. 1967. Growth rates and growth periodicity of tree roots. Int. Rev. For. Res. **2**: 181-236.

MARKS, G. C., N. DITCHBURNE, and R. C. FOSTER. 1968. Quantitative estimates of mycorrhiza populations in Radiata pine forests. Aust. For. **32**: 26-38.

MARX, D. H., A. B. HATCH, and J. F. MENDICINO. 1977. High soil fertility decreases sucrose content and susceptibility of loblolly pine roots to ectomycorrhizal infection by *Pisolithus tinctorius*. Can. J. Bot. **55**: 1569-1574.

MELIN, E., and H. NILSSON. 1957. Transport of C^{14} labelled photosynthate to the fungal associate of pine mycorrhiza. Sven. Bot. Tidskr. **51**: 166-186.

NELSON, C. D. 1964. The production and translocation of photosynthate C^{14} in conifers. *In* The formation of wood in forest trees. *Edited by* M. H. Zimmerman. Academic Press, New York. pp. 243-257.

PERSSON, H. 1978. Root dynamics in a young Scots pine stand in central Sweden. Oikos, **30**: 508-519.

SANTANTONIO, D., R. K. HERMANN, and W. S. OVERTON. 1977. Root biomass studies in forest ecosystems. Pedobiologia, **17**: 1-31.

SCHIER, G. A. 1970. Seasonal pathways of ^{14}C-photosynthate in red pine labeled on May, July and October. For. Sci. **16**: 2-13.

SHIROYA, T., G. R. LISTER, V. SLANKIS, G. KROTKOV, and C. D. NELSON. 1962. Translocation of the product of photosynthesis to roots of pine seedlings. Can. J. Bot. **40**: 1125-1135.

——— 1966. Seasonal changes in respiration, photosynthesis and translocation of the ^{14}C labeled products of photosynthesis in young *Pinus strobus* L. plants. Ann. Bot. (London), **30**: 81-91.

SINCLAIR, W. A. 1974. Development of ectomycorrhizae in a Douglas-fir nursery. I. Seasonal characteristics. For. Sci. **20**: 51-56.

THEODOROU, C., and G. D. BOWEN. 1970. Mycorrhizal responses of radiata pine in experiments with different fungi. Aust. For. **34**: 183-191.

TWAROWSKI, Z. 1963. Investigations on the annual development dynamics of mycorrhizae in 40-year-old spruce stands. Pr. Inst. Badaw. Lesn. **260**: 72-102.

UGOLINI, F. C., H. DAWSON, and J. ZACHARA. 1977. Direct evidence of particle migration in the soil solution of a podzol. Science, **198**: 603-605.

URSINO, D. J., and J. PAUL. 1973. The long-term fate and distribution of ^{14}C photoassimilated by young white pines in late summer. Can. J. Bot. **51**: 683-687.

VOGT, K. A., R. L. EDMONDS, G. C. ANTOS, and D. J. VOGT. 1980. Relationships between carbon dioxide evolution, ATP concentration and decomposition in red alder, Douglas-fir, western hemlock and Pacific silver fir ecosystems in western Washington. Oikos. In press.

WEBB, W. L. 1977. Seasonal allocation of photoassimilated carbon in Douglas-fir seedlings. Plant Physiol. **60**: 320-322.

WEDDING, R. T., and J. L. HARLEY. 1976. Fungal polyol metabolites in the control of carbohydrate metabolism of mycorrhizal roots in beech. New Phytol. **77**: 675-688.

ZIEMER, R. R. 1971. Translocation of ^{14}C in ponderosa pine seedlings. Can. J. Bot. **49**: 167-171.